Studies on Inheritance in Poultry: II. The Factor Black Pigmentation in the White Leghorn Breed.

BULLETIN 161

Agricultural Experiment Station

OF THE

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KINGSTON, R. I., U. S. A., DECEMBER, 1914

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BULLETIN 161, DECEMBER, 1914.

STUDIES ON INHERITANCE IN POULTRY: II. THE FACTOR FOR BLACK PIGMENTATION IN THE WHITE LEGHORN BREED.*

PHILIP B. HADLEY.

It has been shown by Goodale† and by the present writer,‡ and has sometimes been noticed by observant poultrymen, that crosses between the White Leghorn and the White Plymouth Rock breeds of fowl may give rise in F_2 to barred, or otherwise dark colored individuals. This circumstance naturally brings up a question regarding the origin of the black pigmentation necessary for bringing out the barred pattern in F_2. It has been assumed that the White Plymouth Rock fowl does not harbor the factor for black pigmentation, since, whenever black is added to the White Plymouth Rock, as by crossing with a black breed, the barred pattern is manifested. Therefore it has appeared probable that the factor for black pigmentation was present in the White Leghorn. Strong evidence in favor of this view was presented by the present writer in an earlier contribution.‡ But Bateson and Punnett§ have described an instance in

*Contribution 211 from the Agricultural Experiment Station of the Rhode Island State College.

†Goodale, H. D., Experiments with poultry, Proc. Soc. Expt. Biol. and Med., 1910, (7), 178-9.

‡Studies on inheritance in poultry: I. The constitution of the White Leghorn breed, Rhode Island Agr. Expt. Sta., Bul. 155, pp. 151-216, 1913.

§Bateson, Wm., and Punnett, R. C., Report to the Evolution Committee of the Royal Society, IV, pp. 28, 29, Publ., Harrison and Sons, London, 1908.

which two types of white fowl, when mated together, produced progeny, all of which were dark colored, thus suggesting that each type contained one of the two factors whose combination was necessary in order that pigmentation might result. The observation made by Bateson and Punnett naturally suggests the possibility that the White Leghorn does not carry the factor, or factors, for black pigmentation, but contributes only one (X) of two necessary factors, while the White Plymouth Rock contributes the other (Y). This point can be tested by properly devised experimental matings and it is the aim of the present contribution to report the results of an experiment in cross-breeding which has a direct bearing upon it.

The stock used was pure White Leghorn and White Plymouth Rock, line-bred for many generations. The crosses were made in only one direction, White Leghorn ♂ × White Plymouth Rock ♀♀. The majority of the birds were raised to five months of age, and some were kept until they were mature.

Before presenting the experimental results, a word should be said regarding the zygotic constitution of the White Leghorn, since this point has an important bearing upon the interpretation of any results obtained. This breed is characterized by the so-called "dominant white," as contrasted with the "recessive white" present in the majority of other white breeds, including the White Plymouth Rock, White Minorca, and White Silky, for example. In crosses between the White Leghorn and such black fowl as Black Hamburg, Black Minorca, Black Spanish and Black Java, the F_1 birds are invariably white, frequently showing splashes or flecks of black, and less often a barred or partly barred feather. In F_2 the typical Mendelian ratio appears, 3 white : 1 dark. The dark birds comprise both black and barred individuals in the ratio 1 : 3, as stated in an earlier paper.*

One is naturally led to inquire,—What is the nature of the dominant white character in the White Leghorn? The Leghorn white is due to the absence of color, but it is illogical to say that the absence of

*HADLEY, P. B., The presence of the barred plumage-pattern in the White Leghorn breed of fowls. Amer. Nat., 47, 1913, 418–428.

pigment is dominant over its presence. We are forced to conclude that the White Leghorn and other breeds, such as the White Dorking, characterized by the D-white, must contain some pigment-destroying or pigment-neutralizing character which prevents the manifestation of black. The exact nature of this character is unknown, but it may be referred to merely as an inhibiting factor (I), for which the White Leghorn appears to be homozygous. It may be similar to the inhibiting factors (W_1, W_2, W_3, etc.) which Cole* finds present in pigeons.

The manner in which this factor acts, in order to destroy pigment, or to neutralize it, or to prevent its formation, is at present a matter of speculation only. One might assume that there is some fundamental color-substance (C) upon which various color-enzymes act to produce, one black, another red, another buff, etc. Black pigmentation for instance, might be regarded as the result of a color enzyme (N, *nigrum*) acting upon the general color factor C.† Thus, without knowing what factors for pigmentation actually are, it serves our present purpose to assume that one or more factors are necessary for the production of black pigmentation and that the inhibitor, I, through its action upon one or all of them, is able to repress such pigmentation, not only in the White Leghorn itself (provided the factor, or factors, concerned could otherwise determine black pigmentation), but also in F_1 in crosses between the White Leghorn and other breeds characterized by black plumage.

One other character which is possessed by the White Leghorn and which affects the results of crossing in F_2, must be mentioned. This is the barred plumage pattern which, as the writer has already shown,‡ is commonly latent in the White Leghorn stock. The White Leghorn ♂ used in the cross about to be described was homozygous for this character (BB) while the White Plymouth Rock ♀♀ were heterozygous (Bb). In accordance with results of studies on barring, carried

*COLE, L. J., Studies on inheritance in pigeons: I. Hereditary relations of the principal colors, R. I. Agr. Expt. Sta. Bul. 158, 1914.

†DAVENPORT, C. B., Inheritance of characters in the domestic fowl, Publ. No. 52, Carnegie Inst., Washington, 1906.

‡Studies on inheritance in poultry.: I. The constitution of the White Leghorn breed, Rhode Island Agr. Expt. Sta. Bul. 155, pp. 151-216.

on by a number of investigators, it can now be assumed safely that the factor for barring is inherited in a sex-limited manner; that is, the character can be transmitted by the males to both male and female progeny, but the barred females are unable to transmit the pattern to their daughters.

Upon the basis of the assumptions mentioned above, and assuming furthermore, that the factor C embodies all that is necessary (in the absence of I) for black pigmentation, the zygotic formula of the White Leghorn ♂ may be written

$$C_2B_2f_2I_2$$

and that of the White Leghorn ♀ as

$$C_2BbFfI_2.$$

On similar grounds the White Plymouth Rock ♂, lacking all pigmentation factors, would be

$$c_2B_2f_2i_2$$

and the White Plymouth Rock ♀

$$c_2BbFfi_2.$$

In case, however, we make the supposition that two distinct factors are required for black pigmentation, and that only one of these (X) is present in the White Leghorn, while the White Plymouth Rock contains the other (Y), the formula of the White Leghorn ♂ becomes

$$B_2f_2I_2X_2y_2$$

and the White Leghorn ♀

$$BbFfI_2X_2y_2.$$

In a similar manner the White Plymouth Rock ♂ would be represented

$$B_2f_2i_2x_2Y_2$$

and the White Plymouth Rock ♀ as

$$BbFfi_2x_2Y_2.$$

The point at issue therefore is this: Which zygotic formula for the White Leghorn ♂ ($C_2B_2f_2I_2$ or $B_2f_2I_2X_2y_2$), and which formula

for the White Plymouth Rock ♀♀ (c_2BbFfi_2 or $BbFfi_2x_2Y_2$) furnishes the better interpretation for the experimental results now to be reported.

Experimental Results.

In the breeding season of 1912 White Leghorn ♂, 1A, was mated with White Plymouth Rock ♀♀, 270A and 288A. From this mating 63 chicks were hatched and the majority of them raised to the age of five or six months. Of the 63 F_1 birds, five showed imperfect barring in one or more feathers; many possessed feathers slightly flecked with black, indicating that the inhibitor I was not able, when in heterozygous condition, to hold in check all black pigmentation.

In the breeding season of 1913, an F_1♂, 466C, was mated with four of his sisters, 466E, J, M and P. The male was a nearly pure white bird. Of the females, 466E, J and P were pure white, although as a chick 466J showed patches of black down feathers; 466M put up one barred feather among the right secondary coverts.

This mating gave rise to 103 chicks. The majority were reared to the age of five or six months, and some to maturity. Among the 103 birds were 21 which were either dark colored or possessed the barred pattern; in the majority of these the barring was of poor grade, but in a few it was fair.

In the breeding season of 1914, a brother of the male employed in 1913 (466A) was mated with the three females that remained, 466J, M and P. From this mating, 64 birds were hatched and described. Observations showed that 52 were white and 12 barred or dark colored.

Discussion of Results.

If the W. L. ♂ has the zygotic constitution $C_2B_2f_2I_2$ as indicated on a previous page, it forms gametes

$$CBfI \ . \ CBfI$$

while the W. P. R. ♀, c_2BbFfi_2, forms gametes

$$cBfi \ . \ cbFi.$$

The mating would therefore be represented:

$$\begin{gathered} \male \ CBfI \ . \ CBfI \times \\ \female \ cBfi \ . \ cbFi = \\ \hline \female\female \ CcBbFfIi, \text{ white} \\ \male\male \ CcB_2f_2Ii, \text{ white.} \end{gathered}$$

In obtaining F_2, the F_1 cross-bred male possessing the formula CcB_2f_2Ii would form gametes of four sorts as follows:

$$CBfI \ . \ CBfi \ . \ cBfI \ . \ cBfi$$

while the female cross-bred, possessing the formula CcBbFfIi would form gametes of eight sorts:

$$\begin{gathered} CBfI \ . \ CBfi \ . \ cBfI \ . \ cBfi \\ CbFI \ . \ CbFi \ . \ cbFI \ . \ cbFi \end{gathered}$$

The mating would therefore be represented

$\female$ CBfI . CBfi . cBfI . cBfi . CbFI . CbFi . cbFI . cbFi $\times$
$\male$ CBfI . CBfi . cBfI . cBfi =

C_2BbFfI_2 (1), white	$C_2B_2f_2I_2$ (1), white
$C_2BbFfIi$ (2), white	$C_2B_2f_2Ii$ (2), white
$CcBbFfI_2$ (2), white	$CcB_2f_2I_2$ (2), white
$CcBbFfIi$ (4), white	CcB_2f_2Ii (4), white
$\female\female$ c_2BbFfI_2 (1), white	$\male\male$ $c_2B_2f_2I_2$ (1), white
$c_2BbFfIi$ (2), white	$c_2B_2f_2Ii$ (2), white
c_2BbFfi_2 (1), white	$c_2B_2f_2i_2$ (1), white
C_2BbFfi_2 (1), barred	$C_2B_2f_2i_2$ (1), barred
$CcBbFfi_2$ (2), barred	$CcB_2f_2i_2$ (2), barred

This may be summarized:

CHARACTER.	♂	♀	Total.
White	13	13	26
Barred	3	3	6
Total	16	16	32

It is thus apparent that among every 32 F_2 individuals, one would expect to obtain six barred birds, equally divided between the sexes. The results of the 1913 breeding season may now be compared with the expectations as follows:

CHARACTER.	Actual.	Expected.
Barred or dark*.	21	19.4
White.	82	83.6
Totals.	103	103.0

It is apparent that there is close accordance between the expected results and those actually obtained in the 1913 breeding pens. We may, however, consider the second series of matings made in the season of 1914.

CHARACTER.	Actual.	Expected.
Barred or dark.	12	12
White.	52	52
Totals.	64	64

In these data, the experimental and the theoretical results find absolute agreement. It was a matter of chance that exactly 64 birds were raised in the 1914 series.

We may now consider the second possible interpretation of the experimental data. By this hypothesis, it is assumed that the W. L. ♂ contains factor X and the W. P. R. ♀ contains factor Y, both X and Y being required for the manifestation of black. In accordance with this view the W. L. ♂ would possess the formula

$$B_2f_2I_2X_2y_2$$

*When the chicks are young, the barred individuals are invariably dark, and without evident pattern.

forming gametes

$$BfIXy \ . \ BfIXy$$

while the W. P. R. ♀ would be

$$BbFfi_2x_2Y_2$$

forming gametes

$$BfixY \ . \ bFixY$$

The mating would then be represented

$$\begin{array}{c} ♂ \ BfIXy \ . \ BfIXy \times \\ ♀ \ BfixY \ . \ bFixY = \\ \hline ♂♂ \ B_2f_2IiXxYy\text{, white} \\ ♀♀ \ BbFfIiXxYy\text{, white} \end{array}$$

In the production of F_2 the F_1 white cross-bred male, $B_2f_2IiXxYy$, would form gametes of eight sorts:

$$\begin{array}{l} BfIXY \ . \ Bfixy \ . \ BfIXy \ . \ BfixY \\ BfIxy \ . \ BfiXY \ . \ BfIxY \ . \ BfiXy \end{array}$$

while the F_1 white cross-bred female, BbFfIiXxYy, would form gametes of 16 sorts:

$$\begin{array}{l} BfIXY \ . \ Bfixy \ . \ bFIXY \ . \ bFixy \\ BfIXy \ . \ BfixY \ . \ bFIXy \ . \ bFixY \\ BfIxY \ . \ BfiXY \ . \ bFIxY \ . \ bFiXY \\ BfIxy \ . \ BfiXy \ . \ bFIxy \ . \ bFiXy \end{array}$$

This mating would give 128 individuals possessing 27 different zygotic constitutions as follows:

♀♀	♂♂
$BbFfI_2X_2Y_2$ (1), white	$B_2f_2I_2X_2Y_2$ (1), white
$BbFfIiXxYy$ (8), white	$B_2f_2IiXxYy$ (8), white
$BbFfI_2X_2Yy$ (2), white	$B_2f_2I_2X_2Yy$ (2), white
$BbFfIiXxY_2$ (4), white	$B_2f_2IiXxY_2$ (4), white
$BbFfI_2XxYy$ (4), white	$B_2f_2I_2XxYy$ (4), white
$BbFfIiX_2Y_2$ (2), white	$B_2f_2IiX_2Y_2$ (2), white
$BbFfI_2XxY_2$ (2), white	$B_2f_2I_2XxY_2$ (2), white
$BbFfIiX_2Yy$ (4), white	$B_2f_2IiX_2Yy$ (4), white

$BbFfIiXxy_2$ (4), white
$BbFfI_2X_2y_2$ (1), white
$BbFfI_2Xxy_2$ (2), white
$BbFfIiX_2y_2$ (2), white
$BbFfIix_2Yy$ (4), white
$BbFfIix_2Y_2$ (2), white
$BbFfI_2x_2Yy$ (2), white
$BbFfI_2x_2Y_2$ (1), white
$BbFfIix_2y_2$ (2), white
$BbFfI_2x_2y_2$ (1), white
$BbFfi_2x_2y_2$ (1), white
$BbFfi_2x_2Yy$ (2), white
$BbFfi_2X_2y_2$ (1), white
$BbFfi_2Xxy_2$ (2), white
$BbFfi_2x_2Y_2$ (1), white
$BbFfi_2XxYy$ (4), barred
$BbFfi_2XxY_2$ (2), barred
$BbFfi_2X_2Y_2$ (1), barred
$BbFfi_2X_2Yy$ (2), barred

$B_2f_2IiXxy_2$ (4), white
$B_2f_2I_2X_2y_2$ (1), white
$B_2f_2I_2Xxy_2$ (2), white
$B_2f_2IiX_2y_2$ (2), white
$B_2f_2Iix_2Yy$ (4), white
$B_2f_2Iix_2Y_2$ (2), white
$B_2f_2I_2x_2Yy$ (2), white
$B_2f_2I_2x_2Y_2$ (1), white
$B_2f_2Iix_2y_2$ (2), white
$B_2f_2I_2x_2y_2$ (1), white
$B_2f_2i_2x_2y_2$ (1), white
$B_2f_2i_2x_2Yy$ (2), white
$B_2f_2i_2X_2y_2$ (1), white
$B_2f_2i_2Xxy_2$ (2), white
$B_2f_2i_2x_2Y_2$ (1), white
$B_2f_2i_2XxYy$ (4), barred
$B_2f_2i_2XxY_2$ (2), barred
$B_2f_2i_2X_2Y_2$ (1), barred
$B_2f_2i_2X_2Yy$ (2), barred

From this analysis it is apparent that among every 128 individuals 18 would be barred and 110 white, both the barred and the white birds being equally divided between the sexes as follows:

Character.	♂	♀	Total.
White	55	55	110
Barred or dark	9	9	18
Total	64	64	128

It is thus apparent that, among every 128 individuals, one would expect to find 18 barred birds, equally divided between the sexes. The actual results of the 1913 matings may now be compared with these expectations, derived in accordance with the second hypothesis.

CHARACTER.	Actual.	Expected.
Barred or dark	21	14.5
White	82	88.5
Totals	103	103.0

From this tabulation it is clear that there is a wide departure between the actual and the expected results. And when the 1914 data are compared with the expectations derived from this hypothesis, the departure is still more noticeable, since, in the case of the first hypothesis, there was perfect agreement.

The experimental results for 1913 and 1914 may now be brought together and the data compared with the expected results obtained from both hypotheses.

RESULTS.	1913 MATINGS.			1914 MATINGS.			1913–1914 MATINGS.		
	White.	Dark.	Total.	White.	Dark.	Total.	White.	Dark.	Total.
Actual	82.0	21.0	103	52	12	64	134.0	33.0	167
Expected, first hypothesis	83.6	19.4	103	52	12	64	135.8	31.2	167
Expected, second hypothesis	88.5	14.5	103	55	9	64	143.6	23.4	167

From these data it is apparent that the number of dark colored birds actually obtained in the experimental matings of both 1913 and 1914 exceeded the number called for, on the basis of the first hypothesis by only 1.8, while it exceeded by 9.6 the number called for on the basis of the second hypothesis. It is thus conclusively demonstrated that the first hypothesis best explains the phenomena observed. In other words, the White Leghorn carries in itself all the factors necessary for the production of black pigmentation in the F_2 and later generations of crosses with any non-black race.

In thus demonstrating the constitution of the White Leghorn with reference to factors for black pigmentation these results possess a significance in the field of practical breeding. It is not uncommon for poultrymen to employ the White Leghorn in crosses with other breeds to improve certain characters. In so doing it is usually assumed that since the White Leghorn is ostensibly white, and lacking visible pattern, the admixture of Leghorn blood can be made without introducing complexities in either pattern or color. The results of the present study, as well as the experience of many poultrymen, indicate clearly that such a procedure is open to considerable danger if the breeder desires to foster race-purity in his stock. The fact that the White Leghorn carries both black pigmentation and factors for barred plumage pattern means that in F_2 and later generations these characters may appear to the detriment of the breed. Black, which through years of persevering selection has perhaps been eliminated from buff, may be unconsciously re-introduced under the cloak of the Leghorn dominant white. Dark barrings and cuckoo markings, from which a race may have been quite purified, may re-enter under the apparently patternless feathering of this breed. To know the constitution of the race, to know the factors that lie hidden in the germ plasm, as well as those characters that are on parade, enable the intelligent poultryman to make use of desirable characters to the best advantage; and at the same time, to avoid those errors in breeding which result from insufficient knowledge of the fundamental constitution of the race involved.

(OVER)

Description of Plate I.

Figure 1. White Leghorn male, 23 A.

Figure 2. White Plymouth Rock female.

Figure 3. F_1 male from W. L. $\times$ W. P. R. cross.

Figure 4. Type of barred bird obtained in F_2 from W. L. $\times$ W. P. R. cross.

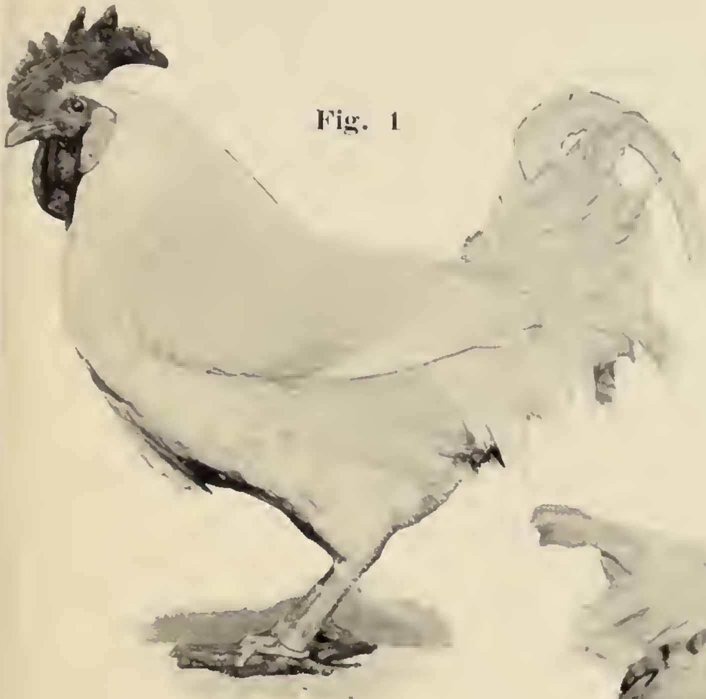

Fig. 1

Fig. 3

Fig. 2

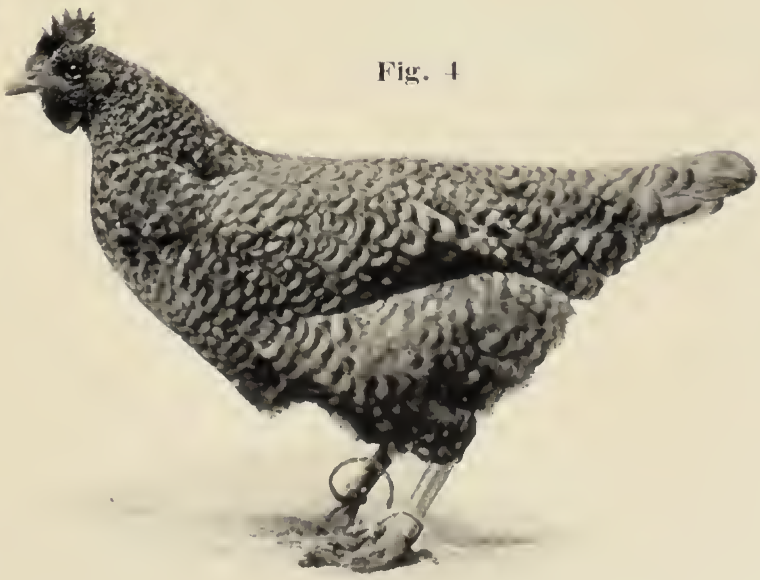

Fig. 4

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